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Male takeover, infanticide, and female countertactics in white-headed leaf monkeys (*Trachypithecus leucocephalus*)

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Abstract Infanticide by males is common in mammalian species such as primates in which lactation lasts much longer than gestation. It frequently occurs in one-male groups following male takeovers and is likely a male reproductive strategy. Reported female countertactics include abrupt weaning of infants, dispersal, or paternity confusion. Here, we estimated costs of female countertactics in terms of weaning ages and interbirth intervals. We observed a population of white-headed leaf monkeys (*Trachypithecus leucocephalus*) in Nongguan Nature Reserve, China (1995–2006) mainly composed of one-male groups. Takeovers ($N=11$) coincided with the peak conception period. Detailed data are presented for five takeovers (34 females, 29 infants, and 47 group-years) leading to six infant disappearances (42.9% of infant mortality). All presumed infanticides were in accordance with the sexual selection hypothesis. Following a takeover, females without infants or with old infants stayed with the new males, incurring no or low costs (via abrupt weaning). Females with young infants dispersing with the old males also experienced low costs. High costs (due to infant loss) were incurred by pregnant females and those with young infants who stayed with the new males indicating that paternity was not confused. Costs in terms of long interbirth intervals were also high for females leaving with the old males to later join the new males, despite infant survival. Female countertactics reflected female philopatry mediated by infant age. Presumably due to the seasonal timing of takeovers, most countertactics seemed successful given that 32.3% of females apparently incurred no costs and 41.2% incurred only low costs.

Keywords Female philopatry · Infant loss · Interbirth interval · Seasonal breeding · Weaning age

Introduction

In the animal kingdom, infanticide by males seems to be a widespread phenomenon occurring in very diverse taxa (Alcock 2001; Ebensperger 1998). It has for example been reported in birds (overview in Veiga 2000), fish (*Pelvicachromis pulcher*, Nelson and Elwood 1997), beetles (*Nicrophorus orbicollis*, Trumbo 2006), and spiders (*Stegodyphus lineatus*, Schneider and Lubin 1996) but is perhaps most frequently documented in the different social systems of mammals (overview, e.g., Ebensperger 1998). It occurs in solitary, seasonally breeding brown bears (*Ursus arctos*, Bellemain et al. 2006), gregarious equids (*Equus caballus*, Cameron et al. 2003; *Equus burchelli*, Pluhacek et al. 2006), and dolphins (*Tursiops truncatus*, Patterson et al. 1998). In all these examples, infanticide was found to be in accordance with the sexual selection hypothesis. This hypothesis postulates that infanticide by males will increase male reproductive success as long as males do not kill their own offspring, the next conception of the infants' mothers is accelerated, and males increase their

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chances of siring the next infants (Hrdy 1974, 1979). The longer the lactation period in relation to gestation, the more time a male can potentially gain for his own reproduction, which is why infanticide in mammals seems to be most frequent in primates and particularly frequent in Old World monkeys (van Schaik and Janson 2000; van Schaik et al. 1999).

On a proximate level, losing an offspring prematurely leads to early resumption of cycling and females conceiving sooner (van Schaik and Janson 2000). This makes a time gain and with it improved reproductive performance for infanticidal males all the more likely. Seasonal breeding does not annul these effects as long as interbirth intervals after surviving infants span more than 1 year (e.g., Bellemain et al. 2006; Borries 1997; Lewison 1998). Even in annual breeders where the interbirth interval cannot be abbreviated, increased chances of conception or improved infant survival are reported or suspected (Enstam et al. 2002; Pereira and Weiss 1991; Wright 1995). These effects can improve the reproductive output of infanticidal males.

In primates, infanticide is common in one-male groups following male takeovers (van Schaik and Janson 2000), when incoming males are almost certainly unrelated to any infants in the groups. But infanticide has also been documented in primate multimale groups, both by newly immigrant and maturing natal males (e.g., Hanuman langurs, Borries 1997; red howler monkeys, Crockett and Janson 2000; sooty mangabeys, Fruteau et al. 2010; chacma baboons, Palombit et al. 2000; and Japanese macaques, Soltis et al. 2000). The past mating history with the infants' mothers is the most likely proximate mechanism for males in assessing paternity probability for infants present or born in the groups (Borries et al. 1999b; Hrdy 1979; van Schaik 2000).

In contrast to unrelated males, females do not gain when their infants are killed. They lose offspring for which the replacement requires extra time and energy which makes the evolution of countertactics very likely (Agrell et al. 1998; Clarke et al. 2009). For example mothers, and also other females and older resident males, could defend the infants (Borries et al. 1999b; Fruteau et al. 2010; Gray 2009; Soltis et al. 2000). Females could preferentially stay in the vicinity of potential defenders, as reported for ursine colobus monkeys (Teichroeb and Sicotte 2008), and reliance on male protection might explain male–female friendships in chacma baboons (Palombit et al. 2000). Alternatively, females could leave the group together with their infants following a takeover (African lions, Packer and Pusey 1983 and purple-faced leaf monkeys, Rudran 1973). However, this option is rare in primates and in most cases in which females emigrated following takeovers, they did so without infants (Sterck and Korstjens 2000). More generally, phylogeny and ecology constrain female dispersal options (Isbell 2004), and it might not be possible to live solitarily or without an adult male. Group splitting might then be an option, as in the case of Hanuman langurs. In this female philopatric species, a group may split after male immigration so that females without infants stay with the immigrant male and females with infants leave with the former resident male (Sugiyama 1965; Winkler et al. 1984).

Female countertactics also depend on infant age (Sterck et al. 2005). If the infant is old enough to survive on its own, it could be left behind (Thomas' langurs, Sterck 1997). A less drastic option is to wean the infant abruptly, even prematurely, without necessarily abandoning it (as in ursine colobus monkeys, Teichroeb and Sicotte 2008). This might lead to suboptimal nutritional conditions early in life that translate into low weaning weight, low resistance to diseases, and increased mortality (Molbak et al. 1994). It might even result in significant differences in life spans, reproductive rates, and lifetime reproductive success (baboons, Altmann 1998). Infants too young to be weaned will put additional constraints on their mothers. To avoid exposing their infants to unrelated adult males, these females should leave with their infants. They could remain with the presumed fathers because these males might protect the infants (Hrdy 1974); but this seems to be rare (Sterck and Korstjens 2000). Pregnant females may resume proceptivity and mate with immigrant males to conceal paternity (van Schaik et al. 1999). Evidence for the success of this tactic is mixed: in Hanuman langurs, the mating pattern of pregnant females does not depend on the identity of the males (Sommer 1994). Once born, infants may be attacked by non-fathers even if they had mated with the mothers during pregnancy (Borries et al. 1999b).

Occasionally, an increased rate of abortions or miscarriages is reported following male takeovers (Hanuman langurs, Agoramoorthy et al. 1988; Sommer 1994; geladas, Beehner and Bergman 2008; Fashing et al. 2009; and Hamadryas baboons, Colmenares and Gomendio 1988). However, due to the relatively high reproductive costs to the female, this response is assumed to be rare in primates (van Schaik et al. 1999) and reports center on only a few species. In sum, theoretical considerations and available evidence suggest that infant age and female reproductive state at the time of a takeover (mediated by constraints on dispersal) are likely to determine female countertactics.

Concerning infanticide in primates, the subfamily Colobinae, particularly the Asian group, has played a prominent role: one of the first published cases of witnessed infanticide in primates (Hanuman langurs, Mohnot 1971; Sugiyama 1965) and one of the first evolutionary approaches to explain the phenomenon (the sexual selection hypothesis, Hrdy 1974) refer to this taxon. Colobines are typically folivorous, and infanticide may be especially frequent in folivorous primates, in which small one-male groups are much more common than in more frugivorous species (Janson and van Schaik 2000). Paternity probability in these small one-male groups can be very high (100% in Hanuman langurs, Launhardt et al. 2001) so that new immigrant males can be rather certain that the infants present in the groups are not their offspring (Borries et al. 1999a). Infanticidal males sired the next offspring of the victims' mothers in a Hanuman langur population studied by Borries et al. (1999a). Indeed, infanticide by males seems to be a regularly occurring phenomenon in Asian colobines. The actual killing of an infant has been observed in black-and-white snub-nosed monkeys (Xiang and Grueter 2007), golden snub-nosed monkeys (Zhang et al. 1999), Hanuman langurs (Newton 1988; Sommer 1994), and Proboscis monkeys (Agoramoorthy and Hsu 2005). Witnessed cases for African colobines stem from red colobus monkeys (Struhsaker and Leland 1985), black-and-white colobus monkeys (Onderdonk 2000), and ursine colobus monkeys (Teichroeb and Sicotte 2008). Furthermore, suspected cases for which only parts of the sequence were witnessed are reported for silvered leaf monkeys (Wolf and Fleagle 1977), purple-faced leaf monkeys (Rudran 1973), and Thomas' langurs (Sterck 1997). In most cases, males were observed to attack infants or infants disappeared shortly after new males immigrated into the groups. Infanticide by males accounts for 30% to 70% of the infant mortality in these populations and is assumed to be a major influence on reproductive tactics and reproductive success for both males and females.

Here we investigated the circumstances of infant disappearances in connection with male takeovers in female philopatric white-headed leaf monkeys (*Trachypithecus leucocephalus*) predominantly living in one-male groups. We estimated potential costs to females by comparing weaning ages and length of interbirth intervals following male takeovers to values for these variables during periods of stable male tenure, proceeding from the assumption that the conditions during stable periods are optimal. We examined if the presence of an infant and its age had an influence on female countertactics, predicting that females (1) without infants stayed with the new males; (2) those with old infants weaned the infants abruptly, the infants survived, and the mothers stayed with the new males; (3) and those with young infants remained with the old male, at least until their infants were weaned. Predictions for pregnant females could not be examined because those largely depend on mating behavior, which was not documented systematically. It therefore is unclear whether paternity could be confused and thus whether pregnant females are expected to stay with the new males or the old males. Finally, we investigated if in the study population the conditions of the sexual selection hypothesis were met.

Materials and methods

Study site

A population of white-headed leaf monkeys was studied at the Nongguan site within the Nongguan Nature Reserve (22°15–17′ N, 107°29–32′ E, 150–430 m a.s.l.), Chongzuo county, Guangxi Zhuang Autonomous Region, China. The climate is mild but seasonal. The mean annual temperature is 22.8°C, and the mean annual precipitation is 1,152 mm (details in Jin et al. 2009a, b). The site consists of about 22 km^2 karstland dominated by limestone hills. Much of the original subtropical, deciduous, broadleaf forest growing on the limestone hills has been replaced by secondary shrub vegetation (up to 5 m in height). Lowland areas and valleys are farmland. There are no villages in the study area. People use the hills to collect firewood and to catch small animals (e.g., snakes or squirrels). The leaf monkeys were rarely seen close to people, the farmland or villages. Crop raiding was never observed. Hunting of monkeys and other animals had been common in the past but has been prohibited since 1998 (Jin et al. 2009b). Extant predators include leopard cats (*Felis bengalensis*), Asiatic golden cats (*Felis temmincki*), yellow-throated martens (*Martes flavigula*), and golden eagles (*Aquila chrysaetos*). Locally extinct are tigers (*Panthera tigris*), leopards (*Panthera pardus*), and clouded leopards (*Neofelis nebulosa*). Predator densities are assumed to be low based on the rarity of sightings but no systematic data are available. The species mentioned here would all be capable of preying at least on juvenile leaf monkeys even though we never witnessed such an event and predator pressure is assumed to be low.

Study population

The leaf monkeys inhabit several of the limestone hills in the northern part of the reserve (see Fig. 1 in Jin et al. 2009b: 207). Each group occupied one or several hills with very little overlap between home ranges of adjacent bisexual groups. On occasion, individuals use ridges to cross the farmland between hills. With 88.3% of the mean annual feeding time spent on leaves, the degree of folivory is comparatively high (Yin et al., unpublished data).

The majority of the bisexual groups (96.3%) were one-male multifemale while multimale groups were rare (3.7%, calculated from Jin et al. 2009b). Similar proportions are reported for another population of the same species (Li and Rogers 2004). Furthermore, 21.9% of all adult males in the population lived in so called non-reproductive groups mainly composed of males of different ages (except infants) and a few immature (but no adult) females (Jin et al. 2009b).

Although infants have been born during all months of the year, births were distributed unevenly throughout the year and 82.0% of all births occurred from December through March (Jin et al. 2009a). Thus, most conceptions must have occurred between June and September based on an estimated gestation length of 6 months. This value was determined for captive Francoise leaf monkeys (*Trachypithecus francoisi*), a closely related species (184 days; *N*=16, Mei 1991). If gestation would, however, be closer to 200 days (i.e., almost 7 months) as reported for other wild Asian colobines (Borries et al. 2011), then the conception peak would last from May to August instead.

Study periods, data collection, and sample sizes

A total of 28 groups have been studied by several observers (see acknowledgements) from 1995 through 2006 for varying durations (Jin et al. 2009b). Takeover frequency and its annual distribution, the percentage of partial takeovers, and the duration of male tenure (definitions below) were calculated based on this largest possible dataset. All other results are based on a subsample of 11 groups, which have been studied for 3 to 11 years (47 group-years total) and group members were individually distinguished. Each month these groups were followed for at least 10 days (mean=18.4±5.8SD; range=10–28) and births, deaths, disappearances, and nipple contact were recorded for all contact days.

In the course of the study 11 takeovers by adult males (definition below) could be documented. Detailed data were available for five of these takeovers, which occurred in four groups. These concerned 34 individual adult females and their 29 infants. For 17 females, the following births could also be documented. Three females with old infants were pregnant at the time of the takeover and thus enter the analysis twice (in relation to the old and the new infant). For comparison, we also present data (weaning age and interbirth interval) during stable tenures for the same groups.

Definitions

Age class definitions follow Rajpurohit et al. (1995) and Jin et al. (2009b) although, the present analysis only deals with infants and adults (fates of juveniles will be presented elsewhere). Leaf monkeys were classified as infants as long as they had nipple contact (mean 19.2 months, Zhao et al. 2008). At the time of takeovers we furthermore distinguished *young* infants (4–14 months) from *old* infants (16+ months) based on the bimodal distribution of infant age due to seasonal breeding. From age 5 years onward females were considered adult (mean age at first reproduction 5.4 years, Jin et al. 2009a). Larger males who had not reached the full head–body length or the shoulder width of an adult male were classified as sub-adults. Adult males had the maximum head–body length and shoulder width.

Following Sterck (1998), a *takeover* occurred when the former resident adult male of a bisexual group was ousted by another male. Unsuccessful takeovers not resulting in permanent group membership changes were rare (assumed twice based on aggressive interactions between males) and were not considered here. We distinguished the *old male* (residing with the females prior to the takeover) from the *new male* (challenging the old male and finally taking over). Note that in all cases the new males appeared to be noticeably younger than the old males even though the “old males” were not necessarily past their prime.

A takeover was considered *complete* if all adult females stayed with the new male once the old male was ousted. In *partial* takeovers, most females stayed with the new male, but at least one female left together with the old male. *Male tenure length* encompassed the time period during which an adult male lived with at least one adult female who was not born during his tenure (Sterck et al. 2005). It was calculated to the month.

The *weaning age* was calculated from the month of birth to the month when nipple contact was last observed (inclusively). The *interbirth interval* lasted from the month of parturition until the month of the next birth. To approximate female reproductive costs, we calculated the interbirth interval back to the female’s last infant that survived its first year of life. Consequently, if an infant was lost prematurely (i.e., during its first year) its birth was not considered resulting in a comparatively long interval. To avoid confusion we introduce the abbreviation *IBI-S* for this measure (with *S* for surviving infants). The longer the IBI-S the higher female reproductive costs. Due to the intermittent nature of our observations, weaning age and IBI-S were calculated to the month.

Data analyses

Weaning ages and IBI-S following takeovers were tested against the control condition during stable male tenures with a Kruskal–Wallis test and a post hoc test based on the α-level reached by the Kruskal–Wallis test (Siegel and Castellan 1988). Infant survival in relation to maternal tactics as well as the sex ratio of presumed infanticide victims compared with the birth sex ratio was tested with a Fisher’s exact test. Annual distributions of infant disappearances and takeover events were tested with circular statistics (Batschelet 1981). Tests were performed in STATISTICA 6.1 (© StatSoft Inc. 1984–2003), and R 2.12.0 using CircStats 0.2–4, and the post hoc test was calculated by hand.

Results

Male takeovers

Of the 11 male takeovers, ten occurred in one-male groups and one in a non-reproductive group (see below). Takeovers were not evenly distributed throughout the year and the majority (ten of 11; 90.9%) took place from May through August (Fig. 1; $r=0.761$, $P<0.001$, Rayleigh test of uniformity, Batschelet 1981). Thus, most new males took over at the beginning of the conception period. Note that the match of takeovers with the peak conception period is improved if the latter is calculated based on 7 months of gestation instead of six. Perhaps as a consequence of this general timing only three (i.e., 12.0%) of the females likely to conceive in the given season (those with no infants or old infants, $N=25$), or 8.8% of all 34 females, were already pregnant at the time of the takeover.

A takeover occurred every 50.1 group-months on average (range, 29–63; $N=9$). When a new male entered the home range of a bisexual group, the old and the new males chased and fought each other, often with high intensity and frequent physical contact. Injuries were common, but we did not witness male deaths during these interactions. In all cases the old male was ousted within less than 2 months. Females were not involved in agonistic interactions between the males and it did not seem as if either of the males aggressively targeted them or their infants. Ousted males withdrew from their groups' home ranges while the new males stayed.

One takeover occurred in a non-reproductive group composed of an older adult male and his presumed offspring: a young adult male, five subadult males, and three young, nulliparous females. These ten individuals had previously split off together from a bisexual group after a takeover (Jin et al. 2009b; Zhao and Pan 2006). When a new adult male invaded, the old male and his presumed oldest adult son often fought him cooperatively. Once defeated, they both disappeared while the subadult males began to move about independently as all-male band. The three nulliparous females stayed with the new male.

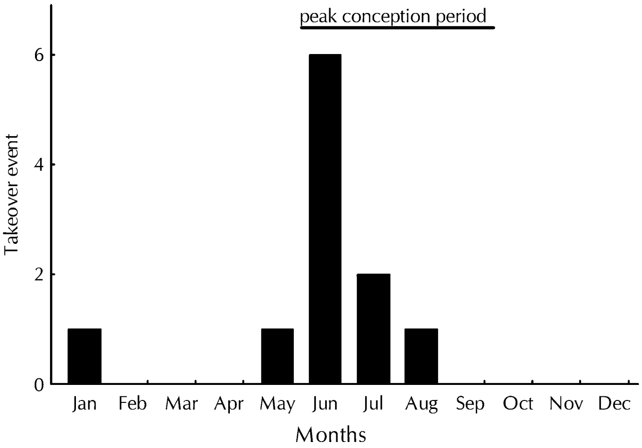

Fig. 1 Annual distribution of male takeovers; plotted are months when takeovers began

Although the exact origin of the new males was unknown, they were neither residents in neighboring groups nor maturing natal males. In most cases ($N=10$) the new males came alone. Only once (in group SHY) did an all-male band of four adult males jointly attack the old male. After the old male was ousted, the group was multimale for 12 months. Thereafter only one adult male remained with the group (Jin et al. 2009b).

Five of the takeovers (i.e., 45.5%) were "complete"; the other six were "partial". Male tenureship length in one-male groups averaged 54.5 months (range, 34–73; $N=8$) and was thus longer than the interval between takeovers (see above) because six old males continued to stay with females (partial takeovers).

Female tactics

Following a takeover, most females stayed with the new males (82.4%, Fig. 2); the rest left the area with the old males. Half of the females who initially left later rejoined their groups and the new males (Fig. 2). In the following, we describe how female reproductive status and infant age

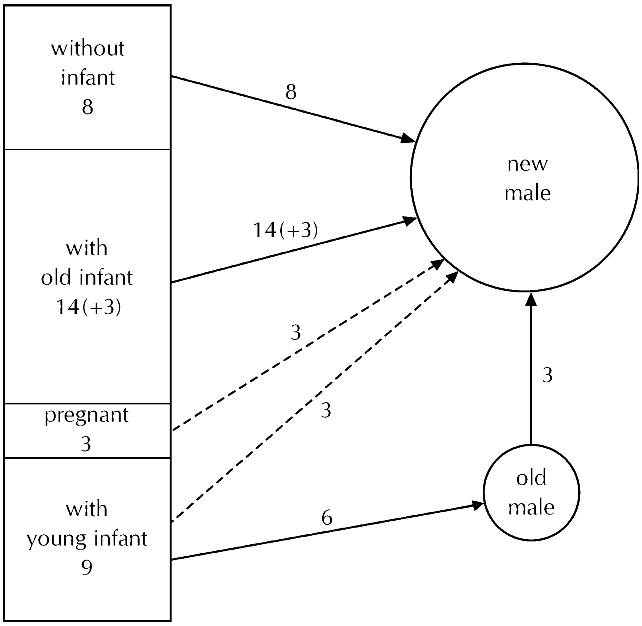

Fig. 2 Females staying with the new or the ousted, old male following takeover (in relation to female reproductive state). The new males stayed in the groups' home range while the old males left the area; numbers represent *N* adult females; we use 14 (+3) to indicate that three of the 17 females with an old infant were again pregnant and are also represented as pregnant females; *solid arrow*, infant survived or no infant; *hatched arrow*, infant loss

might have shaped these female tactics and assess the potential costs in terms of weaning ages and IBI-S.

Weaning age and IBI-S following takeovers

There were 17 females with old infants present during takeovers (Fig. 2). All weaned their infants (rather abruptly) before the takeover was completed at a mean age of 17.7 months. These infants were thus 2.6 months or 12.8% younger than infants weaned during stable tenures (average, 20.3 months; Table 1; Fig. 3). All these old infants survived for at least another year. In addition, nine females with young infants experienced a takeover, of which 66.7% (N=6) left the groups with their infants and the old males and the infants survived. Three of these six females remained and continued to breed with the old males (Fig. 2). They weaned their infants at a younger age compared with stable tenures (mean=17.7 months; i.e., 2.6 months or 12.8% younger; Table 1; Fig. 3). The other three females later joined the new males (Fig. 2) after they had weaned their infants. With a mean age of 18.3 months, these infants were weaned 2.0 months or 9.9% younger than those weaned during stable tenures (Table 1; Fig. 3). All weaning ages following takeovers differed significantly from those during stable tenures (Kruskal–Wallis test $H_{(3,\ N=32)}=18.64$, $P=0.0003$; post hoc test $\alpha<0.001$; significant conditions marked in Fig. 3).

Females with old infants had a mean IBI-S of 24.9 months, which was very similar to the mean interval during stable tenures (24.5 months, Table 1; Fig. 4). Likewise, females with young infants who continued to stay and breed with the old males had similar IBI-S (mean, 24.7; Table 1; Fig. 4). However, females with young infants who later rejoined the new males had longer IBI-S (mean= 31.0 months, i.e., 6.5 months or 26.5% longer) compared with IBI-S during stable tenures (Table 1; Fig. 4). Of the females with young infants who stayed with the new males, one gave birth with an IBI-S of 32.0 months. This was 7.5 months or 30.6% longer than during stable tenures (Table 1; Fig. 4). Finally, three pregnant females stayed with the new males after takeovers. All lost their infants (details below), resulting in a mean IBI-S of 33.7 months, 9.2 months (or 37.6%) longer than intervals during stable tenures (Table 1; Fig. 4). The lengths of the IBI-S following

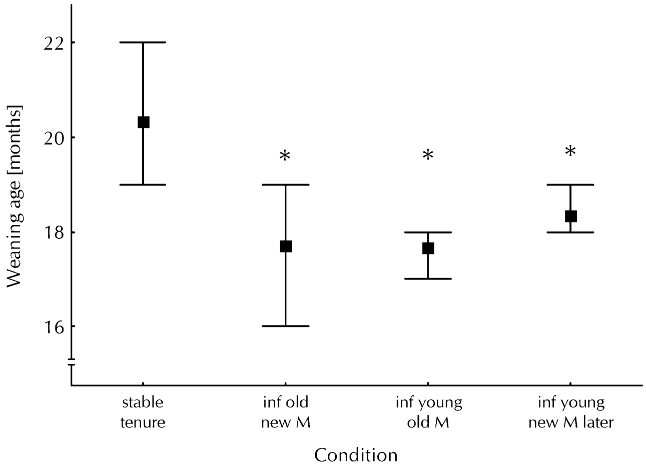

Fig. 3 Mean weaning age under the different conditions; *whiskers*, range; *asterisk*, significantly different from stable tenure (Kruskal–Wallis post hoc test, α=0.001); *inf* infant, *M* male

Table 1 Female countertactics after male takeover and their potential costs in terms of weaning age (current infant) and interbirth interval (to the last infant surviving 1 year)

Condition	*N*	Infant age[a] at takeover	Weaning age			IBI-S (to last infant surviving 1 year)			
			Mean (months)	Median (months)	Range (months)	mean (months)	Median (months)	Range (months)	*N*
With new male	17	Old	17.7	18.0	16–19	24.9	25.0	24–27	7
	3	Young	Infant disappeared			32.0			1
	(3)	(Pregnant)	Infant disappeared			33.7	33.0	33–35	3
	8[b]	No infant							
With new male (later only)[c]	3	Young	18.3	18.0	18–19	31.0	32.0	27–34	3
With old male	3	Young	17.7	18.0	17–18	24.7	25.0	24–25	3
Stable tenure	9		20.3	20.0	19–22	24.5	24.5	24–25	4

Pregnant females in parentheses because they had an unweaned old infant at the time of the takeover too and are thus mentioned twice. For test results see text

[a] Infant age: old=16–19 months; young=4–14 months; pregnant=1–3 months after conception based on the subsequent birth observed

[b] For these eight females, future reproduction could not be documented (three were nulliparous, adults, and for the other five pluriparous females the takeover took place close to the end of the study period)

[c] Initially stayed with the old male

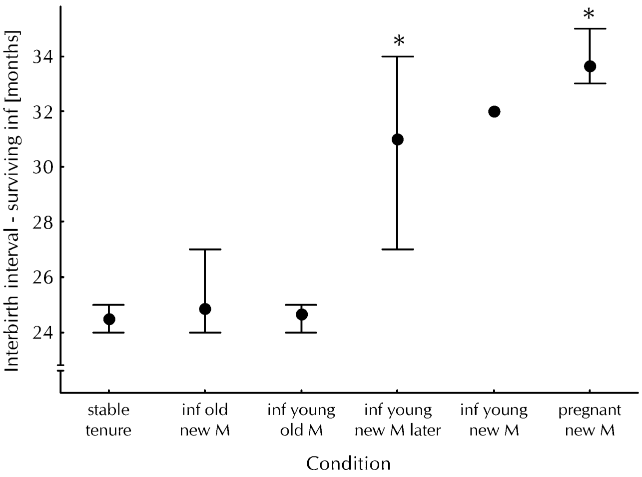

Fig. 4 Mean interbirth interval after a surviving infant under the different conditions; *whiskers* range; *asterisk*, significantly different from stable tenure (Kruskal–Wallis post hoc test, $\alpha=0.02$); *inf* infant, *M* male

takeovers differed significantly from those during stable tenures (Kruskal–Wallis test $H_{(4,\ N=20)}=12.86$; $P=0.012$; post hoc test $\alpha<0.02$; significant conditions marked in Fig. 4; the condition resulting in a single IBI-S was excluded from the test).

Infant loss and presumed infanticides

Of the 17 old infants weaned abruptly after takeovers, three remained with their mothers and the new males and survived. The other 14 dispersed without their mothers and survived. All six young infants who stayed with their mothers and the old males survived, whereas the three young infants who stayed with their mothers and the new males disappeared within 2 weeks after the old males had been ousted, at a mean age of 7.0 months (cases 4, 7, and 8, Table 2). Survival of young infants thus significantly depended on the females' dispersal decision (Fisher's exact test, one-tailed; $P=0.012$). One of these infants (NY) was twice exposed to new males within a few weeks. Initially, when the new male (ZHI) immigrated, the mother and infant left with the old male. When the old male was again ousted by yet another male (CID), the mother and infant rejoined the infant's natal group, where new male ZHI resided. He attacked the infant, but it survived (case 3 in Table 2; see also Wang 2004). Next, the mother and infant rejoined the male who had ousted the old male the second time (CID). He was once observed stalking the infant (case 4), which disappeared the following day.

Three infants were born into groups with new males within 3–5 months after takeovers. Based on a 6-month gestation period, the females must have been pregnant at the time of the takeovers (cases 1, 2, and 6, Table 2). All three infants disappeared within 1–3 months after birth (mean=1.7 months). Another young infant (NP, case 5 Table 2), whose mother was not pregnant, was attacked at the age of 9 months and survived (Wang 2004).

The eight cases described in Table 2 took place in three different one-male groups after the old males had been ousted. Four different males were suspected of infanticide. In the two cases for which we had observations, the infants' mothers defended or rescued the infants either by fleeing the approaching males (thus carrying the infants away) or by attacking them. Other females joined in the defense. Whether female defense delayed infanticide cannot be decided. In three cases, males were observed to stalk and/or attack infants; this includes the one case when the male was observed to bite and injure the infant at the neck (case 3; Wang 2004). It survived the attack but disappeared later (as described above, cases 3 and 4, Table 2). In five of the eight cases, the timing of infant disappearance in relation to a recent male takeover was the main reason we inferred infanticide by males.

Infants were between 1 and 8 months of age (mean=4.3 months; $N=6$) when they disappeared. At least five of

Table 2 Circumstances under which infants were attacked or stalked by new males and infant disappearances following a takeover (cases in chronological order per infant)

Case	Infant name	Infant sex	Infant age at takeover (months)	Date of event/ observation	Infant age at death/ disappearance (months)	Male name	Male observed to	Females defend/rescue	Infant seen with injuries	Infant fate
1	K1	?	Unborn	Feb 2001	1	ZLP		?	No	Disappeared
2	K2	M	Unborn	Apr 2001	3	ZLP		?	No	Disappeared
3	NY	M	7	Sep 24, 2002	Survived	ZHI	Attack and stalk	Yes	Yes	Survived
4				Oct 01, 2002	7	CID	Stalk	Yes	No	Disappeared
5	NP	M	9	Sep 26, 2002	Survived	ZHI	Attack and stalk	?	No	Survived
6	NQ	?	Unborn	Feb 2003	1	CID		?	No	Disappeared
7	NA	M	8	Sep 2006	8	XS		?	No	Disappeared
8	NE	M	6	Sep 2006	6	XS		?	No	Disappeared

the seven suspected targets were males (71.4%), a ratio that did not differ significantly from the significantly biased birth sex ratio of 59.8% male in the study population (Zhao et al. 2009) ($N=122$, Fisher's exact test, one tailed; $P=0.427$). During our study period, 14 infants disappeared prior to weaning. If the six cases of presumed infanticide were indeed infanticides, infanticide would account for 42.9% of infant mortality. Unfortunately, no further comparisons were possible because causes of death were not known for the study population. Population wide, 15.0% of the infants did not survive their first year of life (Jin et al. 2009a). If these data were analyzed separately for stable tenures and takeovers, infant mortality during stable tenures was 7.2% (8 out of 111 infants) and thus significantly lower than the 54.5% after takeovers (six of 11 infants; one young infant already older than 12 months of age excluded here; Fisher's exact test, one tailed; $P<0.003$). Despite the fact that takeovers occurred mainly during the peak conception season, infant disappearances were distributed evenly throughout the year ($r=0.118$; $P<0.831$, Rayleigh test of uniformity, Batschelet 1981, data not shown). This refers to all infant disappearances (the number of losses following takeover was too small to be tested independently).

Discussion

Due to the small sample size (six infants disappeared after a takeover) and the fact that infanticides were only presumed, the results need to be treated with caution, although additional supporting evidence such as attacks and stalking of infants by males were also observed (Table 2). If all presumed infanticides were indeed infanticides, the impact exceeded 40% of the infant mortality in the study population and more than 50% of infants experiencing takeovers in their first year of life did not survive. A similar or even higher impact of infanticide on infant mortality has been reported for other primate species, including both folivores (Hanuman langurs: 31–44%, Borries and Koenig 2000; red howler monkeys: 44–85%, Crockett and Janson 2000; red colobus monkeys: 30.0%, Struhsaker and Leland 1985; ursine colobus monkeys: 71.4%, Teichroeb and Sicotte 2008) and non-folivores (geladas: 57.2%, Beehner and Bergman 2008; white-handed gibbons: 83.3%, Borries et al. 2010; white-faced capuchins: 60.9%, calculated from Fedigan 2003; see also compilation in Janson and van Schaik 2000). These high proportions can be stable if overall infant mortality is low (e.g., red colobus monkeys and our study) or reproductive rates are high (e.g., some *Semnopithecus* populations) but may threaten the survival of small populations (cetaceans: Patterson et al. 1998). The high proportion of infanticides on infant mortality furthermore emphasize the evolutionary importance and the potential impact of infanticide on male and female reproductive success (Agrell et al. 1998; Ebensperger 1998; Hrdy 1979).

Infanticide in white-headed leaf monkeys

The circumstances under which presumed infanticides occurred at our site fit the conditions proposed under the sexual selection hypothesis (e.g., Hrdy 1979). Firstly, new males were probably not related to the victims because they were neither former residents in neighboring groups nor natal males. Furthermore, extra-group copulations have never been observed and are at most rare, perhaps because of the small home range overlap, excellent visibility, and low intruder pressure (low number of extra-group males, Jin et al. 2009b). This will result in high paternity probability for resident males and very low probability for new immigrant males. Unfortunately, however, no paternity data are available for the study population or a closely related species. But in one-male groups of Hanuman langurs at Ramnagar, the old males sired all infants while new males were unrelated to the infants in the groups (Borries et al. 1999a; Launhardt et al. 2001). Second, premature loss of an infant significantly accelerated the subsequent birth generally (Jin et al. 2009a); this holds specifically for infants lost due to presumed infanticide (mean interval till next birth: 10.5 months; range, 8–16; $N=4$). Infanticidal males can thus gain time by reproducing sooner with the mothers. Lastly, the new males' chances of siring the subsequent infants of the victims' mothers must be rated as very high due to the long male tenure (average, 54.5 months) with even the shortest tenure lasting 34 months. Given the presumed high paternity certainty, the new male is likely to father most if not all infants in a group and thus to benefit by infanticide, as in Hanuman langurs at Ramnagar (Borries et al. 1999a).

Seasonal breeding did not prevent infanticide, which is in accordance with data on some other seasonally breeding primates (Borries 1997; Lewison 1998; Pereira and Weiss 1991; Soltis et al. 2000). This is likely because premature infant loss almost always provides a reproductive advantage to males either in terms of subsequently improved infant survival or faster breeding with the infants' mothers. In this connection the timing of male takeovers in the study population seems important: takeovers mainly occurred early in the mating season (Fig. 1), when chances were high that most if not all females would still be cycling. In other seasonally breeding primates, a similar concentration of male dispersal events occurred prior to the mating season (sifakas, Morelli et al. 2009) or during the mating season (Hanuman langurs, Borries 2000; guenons, Cords 2000; Japanese macaques, Sugiyama and Ohsawa 1974).

Estimating costs of female countertactics

A younger weaning age may indicate suboptimal postnatal maternal investment and thus be costly. Nutritional conditions early in life can be strong predictors for lifetime reproductive success, as has been shown for baboons (Altmann 1998). Furthermore, prolonged breast feeding in humans improved the infants' resistance to intestinal problems and significantly lowered infant mortality (Molbak et al. 1994).

As a composite measure of infant survival and speed of reproduction, the IBI-S provides information about any costs in terms of time and energy lost due to failed reproduction. Costs associated with increased IBI-S should typically be more severe than any due to early weaning, especially given seasonal breeding.

Females without infants Following male takeovers, all females without infants stayed with the new males. Unfortunately, however, costs could not be determined as the IBI-S were not known: three females were nulliparous and the other five experienced the takeover at the end of the study period. Conception delays were unlikely, however, because females in a comparable physiological state (those with old infants) had average-length IBI-S following a takeover (Fig. 4). Breeding delays with a new male are also absent in mountain gorillas (Robbins et al. 2009) but significant in Thomas langurs (Sterck et al. 2005) and lions (Packer and Pusey 1983).

Females with old infants Staying with the new male and weaning a current infant abruptly was the tactics employed by all 17 females with old infants (Figs. 2 and 3); all these infants survived. To our knowledge, this is one of the first times that significantly younger weaning ages after takeovers have been documented. Most studies of mating behavior following male takeovers in primates have not included information on the cessation of nipple contact (e.g., Colmenares and Gomendio 1988; van Schaik et al. 1999). One case is reported for wild ursine colobus monkeys and the infant survived despite being weaned at 7 months of age (Teichroeb and Sicotte 2008).

The youngest of the abruptly weaned old infants was 16 months old (Table 1). This is apparently an age at which white-headed leaf monkeys can survive without nipple contact even if they are still significantly younger than infants weaned during stable tenures (Fig. 3). However, we could not detect any adverse effects following this shorter postnatal maternal investment and costs for females were rated as low (Table 3). We note, however, that no data on the infants' performances later in life (such as age at first reproduction, reproductive rate or survival) are available.

At 16 to 19 months of age, these old infants were considerably older than most monkey targets of infanticide (van Schaik 2000). Older targets are also reported for the seasonally breeding Hanuman langurs at Ramnagar (up to 21 months, Borries 1997), where the IBI following a surviving infant was also comparatively long (32 months, Borries and Koenig 2000), so that even the death of an older infant would shorten the time till next conception. However, the oldest infant attacked in our study was only 9 months old (infant NP, Table 2; details below), much younger than the infants weaned abruptly. Rather than providing protection from infanticide, the termination of nipple contact in old infants might mainly signal resumption of cycling to the new male. Comparison of a new male's behavior towards receptive females with or without nursing infant would clarify this issue.

The mean IBI-S value for females with old infants was similar to that for intervals during stable periods (Table 1; Fig. 3); in combination with the younger weaning age, the total costs of takeovers for these females were thus low (Table 3). The ursine colobus female who weaned her infant at 7 months had an IBI-S of 17 months compared with the average of 22 months (Teichroeb and Sicotte 2008). However, this population breeds year round, so the resumption of cycling should be much less restricted than in our study population.

Females with young infants and pregnant females Most females with young infants at the time of takeovers left with the old males, the presumed fathers of the infants. The infants survived but were weaned at a significantly younger age than infants weaned during stable tenures. Early weaning presumably imposes low costs on the mothers who did not face extra costs in terms of IBI-S if they stayed and reproduced with the old males. However, if they joined the new males later, costs were high despite infant survival. In fact, these were the only females experiencing costs in weaning age as well as IBI-S. They joined the new male 7–8 months prior to the next parturition. Based on a 6–7 months gestation period, the new male is likely to have sired the next infant with very little delay. The long IBI-S mainly resulted from the time spent with the old males. Perhaps, as assumed for Thomas' langurs (Sterck 1997), females remaining with a defeated male delay the next conception until after dispersal. Alternatively, only females who did not conceive again left the old males while those who conceived stayed on. Data on female reproductive hormone levels and mating behavior could address these alternative explanations. What remains unclear is why females leaving with the old males still weaned their infants sooner than during stable tenures (at the same age as the abruptly weaned old infants), particularly because subse-

Table 3 Rating of estimated costs for the different female countertactics (relative to stable tenures)

Infant present/infant age	Female	Costs weaning		Costs IBI-S		Overall rating of costs	Infant loss
		Months	Rating	Months	Rating		
Pregnant[a]	With new male			+9.2	H	H	Yes
Yes/old	With new male	−2.6	L	+0.4	0	L	No
Yes/young	With new male			+7.5	H	H	Yes
Yes/young	Disperse With old male	−2.6	L	+0.2	0	L	No
Yes/young	Disperse with old male and with new male later	−2.0	L	+6.5	H	L+H	No

0 average, *L* low, *H* high

[a] At the time of the takeover, these three pregnant females had an old infant which they weaned abruptly; both their infants, i.e., the old one and the still unborn were included in the analysis

quent conceptions did not occur sooner. Early weaning could have been a precaution in case the old males who had already been ousted once were overthrown again by another new male.

In contrast to the predictions, three females with young infants remained with the new males after takeovers, as did the three pregnant females. All lost their infants and had longer IBI-S than those during stable tenures, and thus experienced high costs. While it is generally true that chances for surviving a takeover are low for young infants (van Schaik 2000), the loss of all these infants suggests high paternity certainty. Overall, more than half of the infants experiencing a takeover during their first year of life were lost, a 7.6-fold increase in infant mortality compared with stable tenures (54.5% versus 7.2%). High infant mortality following takeovers is also reported for other primate populations (32 times higher in geladas: Beehner and Bergman 2008; 100% in white-handed gibbons: Borries et al. 2010) and African lions (89.5%, Packer and Pusey 1984). Researchers studying other primates have also reported that infants born soon after takeovers were attacked by males and were either seen dead or disappeared (Tana River red colobus monkeys, Marsh 1979; red colobus monkeys, Struhsaker and Leland 1985; ursine colobus monkeys, Teichroeb and Sicotte 2008). Only rarely have all infants survived takeovers (e.g., Yoshiba 1968, Hanuman langurs). Overall, pregnant females very rarely disperse (Pusey and Packer 1994) even in female dispersal species (Sterck and Korstjens 2000). Still, why do new males behave as if they knew that those infants were unrelated? Similarly, as deduced from sexual interactions, male Hanuman langurs seem to distinguish between female reproductive states (Borries et al. 1999b; Ostner et al. 2006), as do males of other primate species (e.g., chimpanzees, Deschner et al. 2004; long-tailed macaques, Engelhardt et al. 2004) and other mammals (brown bears, Bellemain et al. 2006; feral horses, Cameron et al. 2003). In our study population, these questions can be addressed by a detailed study of sexual behavior in connection with hormonal assessments of female reproductive states.

Female countertactics and their constraints

Most adult females stayed with new males immediately following takeovers. The other three initially stayed with the old males, but then joined the new males, which suggests that philopatry is the preferred female option. Philopatry offers advantages in finding food and can provide the chance for kin support in within and between group competition (Isbell 2004), but it can also be the result of high dispersal costs (Isbell and van Vuren 1996; Sterck 1998). Possible advantages of kin support within groups have yet to be explored for the study population. However, female–female support is probably not important in between group contests in our study population because females rarely participate in between group encounters (Zhao et al., unpublished data).

Females only dispersed when they had young infants and faced threats of infanticide; these attempts to avoid infanticide succeeded. This contrasts with the general dispersal pattern in primate species in which females typically disperse without their infants (Sterck and Korstjens 2000). More recently, however, a few more cases of dispersal to avoid infanticide have been reported (Jack and Fedigan 2009; Morelli et al. 2009; Teichroeb et al. 2009) and previous work has documented other cases of females with infants leaving with an ousted male in Asian colobines (maroon leaf monkeys, Davies 1987; purple-faced leaf monkeys, Rudran 1973; Hanuman langurs, Winkler et al. 1984).

Abrupt weaning was the most common, and most successful, low-cost countertactic for infants which were 16 months or older at the time of takeovers. Overall, male takeovers led to significant costs in 26.5% cases, while 41.2% of females had low costs due to early weaning and

32.3% had no costs. That most tactics were associated with low costs or none could be due to the timing of takeovers in relation to the breeding season.

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References

Agoramoorthy G, Hsu MJ (2005) Occurrence of infanticide among wild proboscis monkeys (*Nasalis larvatus*) in Sabah, Northern Borneo. Folia Primatol 76:177–179. doi:10.1159/000084380

Agoramoorthy G, Mohnot SM, Sommer V, Srivastava A (1988) Abortions in free ranging Hanuman langurs (*Presbytis entellus*)—a male induced strategy? Hum Evol 3:297–308. doi:10.1007/BF02435859

Agrell J, Wolff JO, Yloenen H (1998) Counter-strategies to infanticide in mammals: costs and consequences. Oikos 83:507–517

Alcock J (2001) Animal behavior—an evolutionary approach, 7th edn. Sinauer Associates, Sunderland

Altmann SA (1998) Foraging for survival: yearling baboons in Africa. University of Chicago Press, Chicago

Batschelet E (1981) Circular statistics in biology, 1st edn. Academic, London

Beehner JC, Bergman TJ (2008) Infant mortality following male takeovers in wild geladas. Am J Primatol 70:1152–1159. doi:10.1002/ajp.20614

Bellemain E, Swenson JE, Taberlet P (2006) Mating strategies in relation to sexually selected infanticide in a non-social carnivore: the brown bear. Ethology 112:238–246. doi:10.1111/j.1439-0310.2006.01152.x

Borries C (1997) Infanticide in seasonally breeding multimale groups of Hanuman langurs (*Presbytis entellus*) in Ramnagar (South Nepal). Behav Ecol Sociobiol 41:139–150. doi:10.1007/s002650050373

Borries C (2000) Male dispersal and mating season influxes in Hanuman langurs living in multi-male groups. In: Kappeler PM (ed) Primate males: causes and consequences of variation in group composition. Cambridge University Press, Cambridge, pp 146–158

Borries C, Koenig A (2000) Infanticide in Hanuman langurs: social organization, male migration, and weaning age. In: van Schaik CP, Janson CH (eds) Infanticide by males and its implications. Cambridge University Press, Cambridge, pp 99–122

Borries C, Launhardt K, Epplen C, Epplen JT, Winkler P (1999a) DNA analyses support the hypothesis that infanticide is adaptive in langur monkeys. Proc R Soc Lond B 266:901–904. doi:10.1098/rspb.1999.0721

Borries C, Launhardt K, Epplen C, Epplen JT, Winkler P (1999b) Males as infant protectors in Hanuman langurs (*Presbytis entellus*) living in multimale groups—defence pattern, paternity and sexual behaviour. Behav Ecol Sociobiol 46:350–356. doi:10.1007/s002650050629

Borries C, Savini T, Koenig A (2010) Social monogamy and the threat of infanticide in larger mammals. Behav Ecol Sociobiol. doi:10.1007/s00265-010-1070-5

Borries C, Lu A, Ossi-Lupo K, Larney E, Koenig A (2011) Primate life histories and dietary adaptations: a comparison of Asian colobines and macaques. Am J Phys Anthropol 144:286–299. doi:10.1002/ajpa.21403

Cameron EZ, Linklater WL, Stafford KJ, Minot EO (2003) Social grouping and maternal behaviour in feral horses (*Equus caballus*): the influence of males on maternal protectiveness. Behav Ecol Sociobiol 53:92–101. doi:10.1007/s00265-002-0556-1

Clarke PMR, Pradhan GR, van Schaik CP (2009) Intersexual conflict in primates: infanticide, paternity allocation, and the role of coercion. In: Muller MN, Wrangham RW (eds) Sexual coercion in primates and humans: an evolutionary perspective on male aggression against females. Harvard University Press, Cambridge, pp 42–77

Colmenares F, Gomendio M (1988) Changes in female reproductive condition following male take-overs in a colony of hamadryas and hybrid baboons. Folia Primatol 50:157–174. doi:10.1159/000156343

Cords M (2000) The number of males in guenon groups. In: Kappeler PM (ed) Primate males: causes and consequences of variation in group composition. Cambridge University Press, Cambridge, pp 84–96

Crockett CM, Janson CH (2000) Infanticide in red howlers: female group size, male membership, and a possible link to folivory. In: van Schaik CP, Janson CH (eds) Infanticide by males and its implications. Cambridge University Press, Cambridge, pp 75–98

Davies AG (1987) Adult male replacement and group formation in *Presbytis rubicunda*. Folia Primatol 49:111–114. doi:10.1159/000156313

Deschner T, Heistermann M, Hodges JK, Boesch C (2004) Female sexual swelling size, timing of ovulation, and male behavior in wild African chimpanzees. Horm Behav 46:204–215. doi:10.1016/j.yhbeh.2004.03.013

Ebensperger LA (1998) Strategies and counterstrategies to infanticide in mammals. Biol Rev 73:321–346. doi:10.1111/j.1469-185X.1998.tb00034.x

Engelhardt A, Pfeifer J-B, Heistermann M, Niemitz C, van Hooff JARAM, Hodges JK (2004) Assessment of female reproductive status by male longtailed macaques, *Macaca fascicularis*, under natural conditions. Anim Behav 67:915–924. doi:10.1016/j.anbehav.2003.09.006

Enstam KL, Isbell LA, de Maar T (2002) Male demography, female mating behavior, and infanticide in wild patas monkeys (*Erythrocebus patas*). Int J Primatol 23:85–104. doi:10.1023/A:1013249808137

Fashing PJ, Nguyen N, Kerby JT, Lee LM, Nurmi N, Venkataraman VV (2009) Two group takeovers, infanticide and pregnancy terminations in *Theropithecus gelada* at Guassa, Ethiopia. Am J Phys Anthropol 138:127

Fedigan LM (2003) Impact of male takeovers on infant deaths, births and conceptions in *Cebus capucinus* at Santa Rosa, Costa Rica. Int J Primatol 24:723–741. doi:10.1023/A:1024620620454

Fruteau C, Range F, Noe R (2010) Infanticide risk and infant defence in multi-male free-ranging sooty mangabeys, *Cercocebus atys*. Behav Process 83:113–118. doi:10.1016/j.beproc.2009.11.004

Gray ME (2009) An infanticide attempt by a free-roaming feral stallion (*Equus caballus*). Biol Lett 5:23–25. doi:10.1098/rsbl.2008.0571

Hrdy SB (1974) Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. Folia Primatol 22:19–58. doi:10.1159/000155616

Hrdy SB (1979) Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. Ethol Sociobiol 1:13–40. doi:10.1016/0162-3095(79)90004-9

Isbell LA (2004) Is there no place like home? Ecological bases of female dispersal and philopatry and their consequences for the formation of kin groups. In: Chapais B, Berman CM (eds) Kinship and behavior in primates. Oxford University Press, New York, pp 71–108

Isbell LA, van Vuren D (1996) Differential costs of locational and social dispersal and their consequences for female group-living primates. Behaviour 133:1–36. doi:10.1163/156853996X00017

Jack KM, Fedigan LM (2009) Female dispersal in a female-philopatric species, *Cebus capucinus*. Behaviour 146:471–497. doi:10.1163/156853909X404420

Janson CH, van Schaik CP (2000) The behavioral ecology of infanticide by males. In: van Schaik CP, Janson CH (eds) Infanticide by males and its implications. Cambridge University Press, Cambridge, pp 469–494

Jin T, Wang DZ, Zhao Q, Yin L, Qin D, Ran W, Pan W (2009a) Reproductive parameters of wild *Trachypithecus leucocephalus*: seasonality, infant mortality and interbirth interval. Am J Primatol 71:558–566. doi:10.1002/ajp.20688

Jin T, Wang DZ, Zhao Q, Yin L, Qin D, Ran W, Pan W (2009b) Social organization of white-headed langurs (*Trachypithecus leucocephalus*) in the Nongguan karst hills, Guangxi, China. Am J Primatol 71:206–213. doi:10.1002/ajp.20637

Launhardt K, Borries C, Hardt C, Epplen JT, Winkler P (2001) Paternity analysis of alternative male reproductive routes among the langurs (*Semnopithecus entellus*) of Ramnagar. Anim Behav 61:53–64. doi:10.1006/anbe.2000.1590

Lewison R (1998) Infanticide in the hippopotamus: evidence for polygynous ungulates. Ethol Ecol Evol 10:277–286

Li Z, Rogers ME (2004) Social organization of white-headed langurs *Trachypithecus leucocephalus* in Fusui, China. Folia Primatol 75:97–100. doi:10.1159/000076268

Marsh CW (1979) Female transference and mate choice among Tana River red colobus. Nature 281:568–569

Mei Q (1991) Reproductive cycle of captive black crested langurs (*Presbytis francoisi*) and the growth and development of their offspring. J Beij Teach Coll 12:74–79

Mohnot SM (1971) Some aspects of social change and infant-killing in the Hanuman langur *Presbytis entellus* (Primates: Cercopithecidae) in western India. Mammalia 35:175–198

Molbak K, Gottschau A, Aaby P, Hojlung N, Ongholt L, da Silva APJ (1994) Prolonged breast feeding, diarrhoeal disease, and survival of children in Guinea-Bissau. BMJ 308:1403–1406

Morelli TL, King SJ, Pochron ST, Wright PC (2009) The rules of disengagement: takeovers, infanticide, and dispersal in a rainforest lemur, *Propithecus edwardsi*. Behaviour 146:499–523. doi:10.1163/15683908X399554

Nelson CTJ, Elwood RW (1997) Paternal state and offspring recognition in the biparental cichlid fish *Pelvicachromis pulcher*. Anim Behav 54:803–809. doi:10.1006/anbe.1996.0507

Newton PN (1988) The variable social organization of Hanuman langurs (*Presbytis entellus*), infanticide, and the monopolization of females. Int J Primatol 9:59–77. doi:10.1007/BF02740198

Onderdonk DA (2000) Infanticide of a newborn black-and-white colobus monkey (*Colobus guereza*) in Kibale National Park, Uganda. Primates 41:209–212. doi:10.1007/BF02557802

Ostner J, Chalise MK, Koenig A, Launhardt K, Nikolei J, Podzuweit D, Borries C (2006) What Hanuman langur males know about female reproductive status. Am J Primatol 68:701–712. doi:10.1002/ajp.20260

Packer C, Pusey AE (1983) Adaptations of female lions to infanticide by incoming males. Am Nat 121:716–728. doi:10.1086/284097

Packer C, Pusey AE (1984) Infanticide in carnivores. In: Hausfater G, Hrdy SB (eds) Infanticide: comparative and evolutionary perspectives. Aldine, New York, pp 31–42

Palombit RA, Cheney DL, Fischer J, Johnson SE, Rendall D, Seyfarth RM, Silk JB (2000) Male infanticide and defense of infants in chacma baboons. In: van Schaik CP, Janson CH (eds) Infanticide by males and its implications. Cambridge University Press, Cambridge, pp 123–152

Patterson IAP, Reid RJ, Wilson B, Grellier K, Ross HM, Thompson PM (1998) Evidence for infanticide in bottlenose dolphins: an explanation for violent interactions with harbour porpoises? Proc R Soc Lond B 265:1167–1170. doi:10.1098/rspb.1998.0414

Pereira ME, Weiss ML (1991) Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. Behav Ecol Sociobiol 28:141–152. doi:10.1007/BF00180991

Pluhacek J, Bartos L, Vichova J (2006) Variation in incidence of male infanticide within subspecies of plains zebra (*Equus burchelli*). J Mammal 87:35–40

Pusey AE, Packer C (1994) Infanticide in lions: consequences and counterstrategies. In: Parmigiani S, vom Saal FS (eds) Infanticide and parental care. Harwood Academic Publishers, Chur, pp 277–299

Rajpurohit LS, Sommer V, Mohnot SM (1995) Wanderers between harems and bachelor bands: male Hanuman langurs (*Presbytis entellus*) at Jodhpur in Rajasthan. Behaviour 132:255–299. doi:10.1163/156853995X00739

Robbins AM, Stoinski TS, Fawcett KA, Robbins MM (2009) Does dispersal cause reproductive delays in female mountain gorillas? Behaviour 146:525–549. doi:10.1163/156853909X426354

Rudran R (1973) Adult male replacement in one-male troops of purple-faced langurs (*Presbytis senex senex*) and its effect on population structure. Folia Primatol 19:166–192. doi:10.1159/000155537

Schneider JM, Lubin Y (1996) Infanticidal male eresid spiders. Nature 381:655–656. doi:10.1038/381655a0

Siegel S, Castellan NJJ (1988) Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York

Soltis J, Thomsen R, Matsubayashi K, Takenaka O (2000) Infanticide by resident males and female counter-strategies in wild Japanese macaques (*Macaca fuscata*). Behav Ecol Sociobiol 48:195–202. doi:10.1007/s002650000224

Sommer V (1994) Infanticide among the langurs of Jodhpur: testing the sexual selection hypothesis with a long-term record. In: Parmigiani S, vom Saal FS (eds) Infanticide and parental care. Harwood Academic Publishers, Chur, pp 155–198

Sterck EHM (1997) Determinants of female dispersal in Thomas langurs. Am J Primatol 42:179–198. doi:10.1002/(SICI)1098-2345(1997)42:3<179::AID-AJP2>3.0.CO;2-U

Sterck EHM (1998) Female dispersal, social organization, and infanticide in langurs: are they linked to human disturbance? Am J Primatol 44:235–254. doi:10.1002/(SICI)1098-2345(1998)44:4<235::AID-AJP1>3.0.CO;2-X

Sterck EHM, Korstjens AH (2000) Female dispersal and infanticide avoidance in primates. In: van Schaik CP, Janson CH (eds) Infanticide by males and its implications. Cambridge University Press, Cambridge, pp 293–321

Sterck EHM, Willems EP, van Hooff JARAM, Wich SA (2005) Female dispersal, inbreeding avoidance and mate choice in Thomas langurs (*Presbythis thomasi*). Behaviour 142:845–868. doi:10.1163/1568539055010093

Struhsaker TT, Leland L (1985) Infanticide in a patrilineal society of red colobus monkeys. Z Tierpsychol 69:89–132

Sugiyama Y (1965) On the social change of Hanuman langurs (*Presbytis entellus*) in their natural condition. Primates 6:381–418. doi:10.1007/BF01730356

Sugiyama Y, Ohsawa H (1974) Life history of male Japanese macaques at Ryozenyama. In: Kondo S, Kawai M, Ehara A (eds) Contemporary primatology: proceedings of the fifth international congress of primatology. Karger, Basel, pp 407–410

Teichroeb JA, Sicotte P (2008) Infanticide in ursine colobus monkeys (*Colobus vellerosus*) in Ghana: new cases and a test of the existing hypotheses. Behaviour 145:727–755. doi:10.1163/156853908783929160

Teichroeb JA, Wikberg EC, Sicotte P (2009) Female dispersal patterns in six groups of ursine colobus (*Colobus vellerosus*): infanticide avoidance is important. Behaviour 146:551–582. doi:10.1163/156853909X426363

Trumbo ST (2006) Infanticide, sexual selection and task specialization in a biparental burying beetle. Anim Behav 72:1159–1167. doi:10.1016/j.anbehav.2006.05.004

van Schaik CP (2000) Infanticide by male primates: the sexual selection hypothesis revisited. In: van Schaik CP, Janson CH (eds) Infanticide by males and its implications. Cambridge University Press, Cambridge, pp 27–60

van Schaik CP, Janson CH (2000) Infanticide by males and its implications. Cambridge University Press, Cambridge

van Schaik CP, van Noordwijk MA, Nunn CL (1999) Sex and social evolution in primates. In: Lee PC (ed) Comparative primate socioecology. Cambridge University Press, Cambridge, pp 204–240

Veiga JP (2000) Infanticide by male birds. In: van Schaik CP, Janson CH (eds) Infanticide by males and its implications. Cambridge University Press, Cambridge, pp 198–220

Wang DZ (2004) Social structure of wild white-headed langurs (*Trachypithecus leucocephalus*): a case study at the Nongguan karst hills, Guangxi, China. In: Department of Environmental Biology and Ecology. Beijing University, Beijing

Winkler P, Loch H, Vogel C (1984) Life history of Hanuman langurs (*Presbytis entellus*)—reproductive parameters, infant mortality, and troop development. Folia Primatol 43:1–23. doi:10.1159/000156167

Wolf KE, Fleagle JG (1977) Adult male replacement in a group of silvered leaf-monkeys (*Presbytis cristata*) at Kuala Selangor, Malaysia. Primates 18:949–955. doi:10.1007/BF02382945

Wright PC (1995) Demography and life history of free-ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. Int J Primatol 16:835–854. doi:10.1007/BF02735722

Xiang Z-F, Grueter CC (2007) First direct evidence of infanticide and cannibalism in wild snub-nosed monkeys (*Rhinopithecus bieti*). Am J Primatol 69:249–254. doi:10.1002/ajp.20333

Yoshiba K (1968) Local and intertroop variability in ecology and social behavior of common Indian langurs. In: Jay PC (ed) Primates: studies in adaptation and variability. Holt, Rinehart and Winston, New York, pp 217–242

Zhang S, Liang B, Wang L (1999) Infanticide within captive groups of Sichuan golden snub-nosed monkeys (*Rhinopithecus roxellana*). Folia Primatol 70:274–276. doi:10.1159/000021707

Zhao Q, Pan W (2006) Male-immature interactions seem to depend on group composition in white-headed langur (*Trachypithecus leucocephalus*). Acta Ethol 9:91–94. doi:10.1007/s10211-006-0019-1

Zhao Q, Tan CL, Pan W (2008) Weaning age, infant care, and behavioral development in *Trachypithecus leucocephalus*. Int J Primatol 29:583–591. doi:10.1007/s10764-008-9255-8

Zhao Q, Jin T, Wang DZ, Qin D, Ran W, Pan W (2009) Lack of sex-biased maternal investment in spite of a skewed birth sex ratio in white-headed langurs (*Trachypithecus leucocephalus*). Ethology 115:280–286. doi:10.1111/j.1439-0310.2008.01609.x